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Critical Literature Review
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***Southern Ocean acidification and the effect on pteropods
and krill***

Briar Schwalger-Smith

Student ID: 95623881

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Increasing anthropogenic carbon dioxide in the atmosphere decreases the pH of the ocean and the carbonate ion concentration. Colder temperatures and winds causing the upwelling of deep sea water are two factors that will increase the rate of ocean acidification in the Southern Ocean, relative to lower latitudes. Pteropods and krill are both important species in Antarctic ecosystems and this review outlines the current understanding of how they are affected by projected changes to ocean chemistry. All species of thecosomata (shelled pteropod) experienced degrees of shell dissolution as a result of ocean acidification and aragonite undersaturation. Other physiological factors and survival rate varied between pteropod species but predominately showed a negative impact. Aragonite undersaturation is projected to occur in the Southern Ocean by 2050 and by 2030 in winter. The effects of ocean acidification on pteropods have been more widely researched than the effects on the key ecosystem species, krill. Increased carbon dioxide levels detrimentally affected the hatch rate of krill eggs and population collapse is projected for 2300, with severe and widespread consequence to the entire ecosystem. This review highlights current gaps in the research and identifies the urgent need for a more comprehensive understanding of the ecological impacts of declining or disappearing pteropod and krill populations.

Contents

Introduction.....	3
Pteropods in the Southern Ocean.....	4
The Effects of Ocean Acidification on Pteropods.....	4
Krill in the Southern Ocean.....	6
The Effects of Ocean Acidification on Krill.....	7
Discussion and Direction for Future Research.....	7
Conclusion.....	9
References.....	10

Introduction

Ocean acidification is an effect of increased levels of atmospheric carbon dioxide due to human activity. As CO₂ from the atmosphere is absorbed by the ocean, the concentration of hydrogen ions increases. Simultaneously, the concentration of carbonate ions decreases. The interaction between the levels of absorbed anthropogenic CO₂, reduced pH and lower calcium carbonate (CaCO₃) saturation has been well verified with models and hydrographic surveys, particularly in surface waters where the majority of ocean production occurs (Feely et al., 2004; Khatiwala, Primeau, & Hall, 2009; Orr et al., 2005). Our understanding of how marine systems are affected by anthropogenic CO₂ has lagged behind our knowledge of terrestrial environments. In the past the marine ecosystems in the Southern Ocean has been considered to be somewhat “buffered” from the rest of the world’s oceans and the human influences by the physical barrier provided by the Antarctic circumpolar current (ACC). However in reality, this ocean is just as porous as other oceans (Aronson, Thatje, McClintock, & Hughes, 2011) and factors such as the colder temperatures and surface winds causing upwelling of deep sea water make the Southern Ocean particularly susceptible to ocean acidification, relative to lower latitudes (Doney, Fabry, Feely, & Kleypas, 2009; McNeil & Matear, 2008; Orr et al., 2005). The Southern Ocean absorbs ~40% of the anthropogenic CO₂ produced worldwide (Khatiwala et al., 2009) and there has been a steady decrease in pH of 0.02 units per year for the last 30 years, contributing to a total decrease of 0.1 pH units since pre-industrial times (Orr et al., 2005). Although this may appear to be a minor change, this pH change and the associated decrease in carbonate ion (CO₃²⁻) concentration represent a significant change in the ocean’s chemistry. Effects of ocean acidification in the Southern Ocean will include the effects of climate change seen in other marine systems in the world, such as altered food web dynamics, shifts in distribution of species and an overall decrease in ocean productivity (Hoegh-Guldberg & Bruno, 2010).

This review will examine the effects of ocean acidification on two important species in the Southern Ocean, pteropods and krill. These two species were chosen as they represent two dominant zooplankton species in different Antarctic ecosystems and they are affected by ocean acidification in different manners. Early research on the effects of ocean acidification has focussed on calcifying organisms such as pteropods, however recent research has also investigated the impact on the key Antarctic species, krill.

Pteropods in the Southern Ocean

Pteropods snails are approximately 1 cm in size and are widely distributed components of the Southern Ocean ecosystem, seasonally exceeding the total biomass of krill in some regions (Hunt et al., 2008). In contrast to many other molluscs, pteropods spend their entire lifecycle in pelagic regions and are mostly commonly found to depths of 200 m. Shelled pteropods are herbivorous and form an integral part of Southern Ocean food webs as a food source for zooplankton, fish, whales and birds (Gazeau et al., 2013). The density of pteropods can reach thousands of individuals per cubic metre and therefore they have a significant influence on carbon flow in the ecosystem (Aronson et al., 2011; Hunt et al., 2008). Southern ocean pteropods fall into two orders; Thecosomata (shelled pteropods) and Gymnosomata (naked pteropods). Most of the research on Southern Ocean pteropods focuses on the thecosomatous species, particularly the most dominate *Limacina helicina antarctica*. They are considered to be a good overall indicator of marine ecosystem health (Brad A. Seibel & Dierssen, 2003).

The Effects of Ocean Acidification on Pteropods

Shelled pteropods are one of the few pelagic species that makes its shell exclusively from aragonite, a form of calcium carbonate with a rapid dissolution rate. Low carbonate ion concentration, partnered with low temperatures, makes calcification an energetically costly exercise for organisms. Pteropods in the Southern Ocean currently live in areas of carbonate concentration and temperature close to the energetic limit of their ability to secrete shells (Aronson et al., 2011; McClintock et al., 2009). They are therefore very susceptible to the effects of ocean acidification which can adversely affect their ability to form and maintain shells.

Using a 'business-as-usual' scenario for future CO₂ emissions, projections suggest that the upper Southern Ocean will become undersaturated with respect to aragonite by 2050, extending throughout the Southern Ocean by 2100 (Orr et al., 2005). More recent research by McNeil and Matear (2008), show that wintertime aragonite undersaturation in the upper ocean is projected to occur by 2030. The effects of undersaturation of aragonite on pteropods have been investigated primarily through laboratory incubations at increased partial pressures of CO₂ (pCO₂) corresponding to future atmospheric projections. Signs of shell dissolution in acidified conditions were first reported in the Subarctic Pacific species, *Clio pyramidata*, by Orr et al. (2005). Further studies on juvenile and adult *Limacina helicina* have all reported a negative impact on calcification and shell growth as a function of decreasing pH, when considering a pH drop of less than 0.4 units (Nina

Bednaršek et al., 2012; Comeau, Jeffree, Teyssie, & Gattuso, 2010; Lischka, Büdenbender, Boxhammer, & Riebesell, 2011). The level of shell dissolution corresponds strongly to incubation time. In the Arctic species, *Limacina helicina*, the decrease in calcification was highly correlated to the decrease in aragonite saturation. Contrary to some other studies, this species was able to precipitate calcium carbonate to form a shell at low saturation levels, however model predictions by Comeau et al. (2009) suggest that this pteropod will be unable to calcify in the Arctic by end of the century. This model did not take into account the simultaneous shell dissolution which would likely accelerate the decrease in calcification (Nina Bednaršek et al., 2012). It did, however, demonstrate that calcification at low saturation levels can vary between pteropod species and the situation is potentially more complex than initially thought.

Seasonal variability of carbonate ion concentration and decreasing pH is likely to adversely affect the Antarctic species *Limacina helicina* first, as key larval development occurs during winter months (McNeil & Mearns, 2008). There have been no studies on the lifecycle of Antarctic pteropod species, however studies on relevant pteropod species suggest a lifecycle of 1-2 years (Hunt et al., 2008). Further research has proposed that the seasonal variation of aragonite in Antarctic waters is much greater than the average variation that has occurred since pre-industrial times. If the Antarctic pteropod does in fact have a lifecycle of over a year, this suggests that the pteropod could be more resilient to aragonite variation than expected and has been previously reported (McNeil, Sweeney, & Gibson, 2011). This represents an area for further investigation.

In 2012 research reported the first example of live specimens of *Limacina helicina antarctica* collected in the Southern Ocean to exhibit shell dissolution (N Bednaršek et al., 2012). The samples were collected in a region of upwelling where deep sea water, which is naturally lower in aragonite concentration, mixes with surface water that has absorbed anthropogenic CO₂. Regions of wind driven upwelling are expected to increase under a 'business-as-usual' climate model for the next century (Le Quéré et al., 2007). The two-tiered effect of increased upwelling and further surface water absorption of atmospheric CO₂ will increase the regions of threat to pteropod populations.

The effects of ocean acidification on processes other than calcification have received less attention. Studies on respiration and survival with respect to ocean acidification have produced some variable results. In the species *Limacina helicina antarctica*, respiration decreased at elevated pCO₂ by 20-25% (Fabry, Seibel, Feely, & Orr, 2008; B. A. Seibel, Maas, & Dierssen, 2012). This metabolic suppression would likely affect the growth and reproductive potential of the pteropod by decreasing

the rate of processes such as protein synthesis. In contrast, respiration in the Arctic species *Limacina helicina* was not affected by changes in pH at ambient temperatures, however at elevated temperatures respiration increased linearly with decreasing pH (Comeau, Jeffree, et al., 2010). These studies show that the response of Arctic and Antarctic pteropods can differ and previous assumptions based on one species may not necessarily hold for all pteropods. Recent research on the pteropod *Limacina helicina antarctica* showed that respiration was influenced by long-term feeding and the abundance of phytoplankton (B. A. Seibel et al., 2012). Therefore pteropods may be directly affected by ocean acidification through CO₂ induced suppression of respiration and indirectly by changing phytoplankton population as a result of climate change (B. A. Seibel et al., 2012). Physiological responses to increased pCO₂ is complex and influenced by a combination of factors including temperature, phenotypic history and baseline metabolism (Gazeau et al., 2013).

Antarctic Krill in the Southern Ocean

Antarctic krill (*Euphausia superba*; hereafter krill) is a pelagic species, like pteropods, and has the largest total biomass of all species in the Southern Ocean. It is a small, swimming crustacean that lives in large swarms and can reach densities of greater than 10,000 individuals per cubic metre (Hamner & Hamner, 2000). It is a key Antarctic species that feeds directly on phytoplankton and supports a commercial fishery and a high biomass of predators including baleen whales, fish, seals and penguins (A. Atkinson, Ward, Hunt, Pakhomov, & Hosie, 2012). The distribution of krill is highly uneven with over 70% of stock in the Atlantic sector (0 - 90°W). Overall 87% of krill occupy regions over deep (>2000 m) ocean water (A Atkinson et al., 2008). The main spawning cycle of krill occurs in summer from January to March. Throughout their lifecycle, krill are found in a range of water depths and migrate vertically and horizontally over different time cycles. They spawn eggs at the surface and these sink to depths of 700 – 1000 m before larvae hatch and migrate back to the surface in a cycle that takes approximately 30 days (S. Kawaguchi et al., 2011). Krill already experience high and variable CO₂ concentration during vertical migration, however the sensitivity of krill development is not fully understood and will be vital knowledge as the effects of climate change continue to impact on the Southern Ocean (S. Kawaguchi et al., 2011). Krill already face stressors from temperature changes, decreasing sea ice and changes in phytoplankton production. It is therefore vital that the effect of changing pH is fully understood and can be incorporated into projections for the krill population.

The Effects of Ocean Acidification on Krill

Recent research investigated the effect of elevated CO₂ levels on the hatch rate of krill eggs. Kawaguchi et al. (2013) focussed on the embryonic and larval stages as they are thought to be more environmentally sensitive than adult krill. Exposure of embryos to conditions above 1,250µatm pCO₂ detrimentally affected hatch rate, slowed embryonic development and almost completely inhibited hatching at a level of 2,000µatm pCO₂ (S Kawaguchi et al., 2013). It is noted that even if hatching occurs in projected future scenarios, this may not necessarily facilitate survival. If development is slowed as a consequence of higher pCO₂ in deep water, krill larvae may not be able to swim back to the surface before using up their internal energy supply. The details of how embryonic development may be affected by increased pCO₂ are not yet understood. The Weddell Sea and the Haakon VII Sea are important krill habitats and projections show these regions could become high risk areas for krill hatching and development within a century (S Kawaguchi et al., 2013). Under the 'business-as-usual' scenario for future CO₂ emission, the Southern Ocean krill population could face collapse by 2300, as pCO₂ in the ocean reaches a level that does not support hatching or development (S Kawaguchi et al., 2013).

Experiments with adult krill have demonstrated increased CO₂ concentration can alter internal acid-base regulation and induce greater energy requirements, as observed through the increase metabolic rate, ingestion and nutrient release. This is likely to negatively affect krill populations in winter months when food supply is less abundant (Saba, Schofield, Torres, Ombres, & Steinberg, 2012).

The effects of ocean acidification on calcification in pteropods have been reasonably well researched, as outlined above, however the effect on the rate of calcification of the chitinous crustacean exoskeleton of krill is unknown (Flores et al., 2012). Krill produce and moult their exoskeleton a number of times during their life. This cycle is dependent on chemical and physiological processes which allow the uptake of elements such as calcium to build the exoskeleton. As yet, there has been no research into how ocean acidification may affect these processes in krill.

Discussion and Direction for Future Research

Research indicates that the effects of ocean acidification on both pteropods and krill will be complex and significant in the Southern Ocean ecosystem. Early research on ocean acidification identified pteropods as a particularly vulnerable species due to their aragonite shell. Shell dissolution

represents a basic chemical reaction and was therefore one of the most obvious potential effects of decreasing pH in the ocean as a result of anthropogenic CO₂ emissions. There is a large body of research on the effects of projected pCO₂ levels on shelled pteropod species in polar regions. There is less research available on aspects other than calcification for pteropods. It has long been known that krill are a keystone species in marine ecosystems and research has been completed investigating aspects of their lifecycle, regional variation and distribution (Flores et al., 2012). Thus far, there is a relatively small amount of research identifying the effects of ocean acidification on krill. For both species, there remain a number of areas that require further attention in order to better understand the implications of ocean acidification.

A declining pteropod population would be likely to have severe effects on the predators that depend on them, however there is a lack of research in this area and the impact on other Antarctic organisms has not been investigated. Pteropods are both consumers and prey within Antarctic ecosystems and there is a need for further research into their population structure and seasonal variation in the Southern Ocean in order to better understand these roles.

All calcification studies on pteropod species have supported the relationship between decreasing pH and shell dissolution, however no investigations into how this shell dissolution affects physiological processes have been completed. These factors may accelerate the effects of ocean acidification on the pteropod population and it is therefore important that they are understood. Research on survival rates has produced variable results and has shown that shell dissolution is not necessarily fatal. It is feasible that calcification on the inside of the shell may counteract the shell dissolution on the exterior, however the majority of experiments so far show a net loss of shell due to the rapid rate of dissolution (N Bednaršek et al., 2012). The decrease in shell mass may make the pteropods more vulnerable to predators. Potential effects of climate change include the migration of pteropods northward or the establishment of species, usually associated with lower latitudes, in Antarctic waters. This could expose pteropods to shell-crushing predators not previously encountered. When Mediterranean pteropod species were exposed to aragonite undersaturation they showed lower shell growth and malformations, however they were viable and had a normal development (Comeau, Gorsky, Alliouane, & Gattuso, 2010). Further research on the *Limacina helicina antarctica* to address the viability and survival rates in individuals with different degrees of shell degradation is important for a more detailed understanding of the future effects.

The impact of ocean acidification on Southern Ocean krill and the projected collapse of the krill population by 2300 (S Kawaguchi et al., 2013) would have catastrophic effects on the entire Antarctic ecosystem. Decreases in hatch rate and the overall biomass of krill would most severely

affect species that are unable to switch to alternative prey. Future research into the resultant effects from the removal of krill from the Southern Ocean is essential. It is also important that the effects of ocean acidification on larvae development and adult krill physiology are investigated. Potential negative impacts on these aspects may demonstrate that the projected time frame for population collapse is too conservative and may occur earlier than 2300. This has implications for the management of this fishery and is therefore vital knowledge.

Conclusion

Both pteropods and krill are important species in the Antarctic ecosystems. Ocean acidification has direct effects on these species through shell dissolution, decreases calcification, suppressed embryonic development and changes to physiological processes. The indirect and cumulative effects of ocean acidification are not fully known and represent some of the areas for further research. The projections of future changes to the ocean's chemistry from anthropogenic CO₂ emissions, and the corresponding decline in pteropod and krill population, could have dire consequences for a large number of dependent Antarctic species. The effect of Southern Ocean acidification has already been observed in live pteropods, a species which is often referred to as a good overall indicator of ecosystem health. This highlights the urgent need for a more comprehensive understanding of the ecological impacts of declining or disappearing pteropod and krill populations.

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